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Jays and oaks

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in the face of jay pressure. Thus both pressures in combination might have contributed to the size and form of the oak seedlings' root system.

The jay's bill structure, feeding technique and preference for acorns form an interlinked, adaptive complex. Some of the factors which might have selected for this have been discussed previously in this chapter. In addition to these, timing of breeding may also be the result of a prolonged interaction between jays and oaks. The nestling period (see also HOLYOAK, 1967) coincides rather precisely with the peak occurrence of caterpillars which defoliate oaks. Furthermore the supply of oak seedlings with good cotyledons is highest in the period of fledgling care.

In sum then, several features of oaks and jays fit extremely well. These at least partly evolved as a consequence of mutual selective pressures and resulted in the co-adapted features that are apparent in the present day symbiosis between jays and oaks.

SUMMARY

The European jay (*Garrulus g. glandarius*) strongly depends on acorns for food. Many acorns are hoarded enabling the jay to feed upon them at times of the year in which they would otherwise be unavailable. Many of the hoarded acorns germinate and become seedlings so that jays play an important role in the dispersal of acorns and the reproduction of oaks (in this study: *Quercus robur*, the pedunculate oak). These mutual relationships were analysed both with wild jays in the field (province of Drente, The Netherlands) and with tame birds in confinement.

Variation in the composition of the food throughout the year is described quantitatively. Acorns were the stock diet of adults in most months of the year. Leaf-eating caterpillars predominantly occurring on oak were the main food items of nestlings. Acorns formed the bulk of the food of fledglings in June.

A high rate of acorn consumption in winter, spring and early summer becomes possible because individual jays hoard several thousands of acorns, mainly in October. In experiments, acorns of pedunculate oak were not preferred over equal sized acorns of sessile oak (which was not found in the study area). Acorns of pedunculate oak were strongly preferred over those of American oak and nuts of hazel and beech. Among acorns of pedunculate oak, ripe, sound, long-slim and big ones were preferred. Jays collect one or more (up to six) acorns per hoarding trip. In the latter case, the first ones are swallowed and the last one is usually carried in the bill. For swallowing the dimensions of the beak imposed a limit on size preference; for bill transport usually the biggest acorn was selected.

The greater the number of acorns per trip, the longer was the transportation distance during hoarding. From trip to trip jays dispersed their acorns widely and when several acorns were transported during one trip, these were generally buried at different sites. Burial took place by pushing acorns in the soil and by subsequent hammering and covering. Jays often selected rather open sites, transitions in the vegetation and vertical structures such as saplings and tree trunks, for burial of acorns. In captivity jays also hoarded surplus food. Here, spacing out of burials was also observed; previously used sites usually being avoided. In addition, hiding along substrate edges and near conspicuous objects was observed. Jays tended to hide near sticks presented in a horizontal position rather than near identical ones in vertical position, especially when the colour

of the sticks contrasted with the colour of the substrate. Also, rough surfaced substrate was strongly preferred over similar but smooth surfaced substrate.

Successful retrieval of and feeding on hoarded acorns were observed in winter even when snow-cover had considerably altered the scenery. No evidence was obtained that acorns could be traced back by smell. Many indications were obtained that visual information from near and far beacons, memorized during hiding, was used in finding acorns. The use of beacons by captive jays was also studied. Experiments led to the conclusion that vertical beacons are more important to retrieving birds than identical horizontal ones. The discrepancy with the jay's preference for horizontal structures during hiding is discussed.

Most seedlings emerge in May and June. The distribution pattern of seedlings and bill prints on the shells of their acorns indicated that many seedlings emerged from acorns hidden by jays in the previous autumn. The cotyledons of these plants remain underground and are in excellent condition in spring and early summer. Jays exploited acorns by pulling at the stem of seedlings and then removing the cotyledons. This did not usually damage the plants severely. Jays can find acorns in this situation partly because they remember where they buried acorns. In addition, it was shown that jays select seedlings of oak rather than ones of other species, and that they preferentially inspected those seedlings that were most profitable in terms of cotyledon yield and quality. Experiments uncovered some of the visual cues used in this discrimination.

The effects of hoarding on the preservation of acorns were examined in the field and the laboratory. Being buried reduced the chance that acorns were robbed by conspecifics and other acorn feeders. Scatter hoarding did not lead to better protection of buried acorns than larder hoarding, but the spread of risk was better in the former than the latter. It was concluded that the way in which jays hoard acorns increases the chance that they can exploit them later. In addition, the condition of acorns is better preserved by being buried.

An analysis was made of the consequences of the jay's behaviour for oaks. The oak does incur certain costs: some of its acorns are eaten by jays during the dispersal and storage phase, and some seedlings are damaged as a consequence of cotyledon removal. However, these costs are outweighed by the benefits the oak receives. Many of its most viable acorns are widely dispersed and buried at sites where the prospects for further development into mature oak are highly favourable.

The adaptiveness of the characters involved in preferential feeding on and hoarding of acorns by jays is discussed in relation to several environmental pressures: competition with allied species; food fluctuations in the jay's niche; and food competitors better equipped to break up hard "dry" fruits.

Reversely, jays exert several selective pressures which are likely to have evolutionary consequences for oaks, such as the selection of long-slim and large acorns with tight shells. In addition, oak seedlings with a long tap root and tough stem are selected for.

Although other factors than mutual selective pressures between the two may have affected the present day fit between jays and oaks it is concluded that several characters of jays and oaks can be considered as co-adapted features of a symbiotic relationship.

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